NEW CHARACTERS TO DIFFERENTIATE THE ANT GENERA LASIUS F. AND FORMICA L. (HYMENOPTERA: FORMICIDAE)

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Introduction and history

Ants of the genera *Formica* and *Lasius* are among the most dominant and abundant in the Holarctic region, and form a large and important fraction of the fauna. Strangely for such important insects, the characters currently used to differentiate the two genera are vague and often misleading, resulting in difficulty in identification and indeed in misidentification at generic level.

Mayr (1861) published the first dichotomous key to the worker caste of *Formica* and *Lasius*. To separate the two he used the relative size of the funicular segments, the form of development of the ocelli and the shape and degree of distinctiveness of the frontal triangle. Forel (1874) added to these characters the shape of the frontal carinae, the variable numbers of maxillary palp segments, the relative position of the petiole scale, the shape of the alitrunk,

the length of the legs and shape of the proventriculus.

Emery (1925) introduced the shape of the propodeal spiracles as a differentiating character, and dismissed all the other, earlier-

a differentiating character, and dismissed all the other, earlier-mentioned characters. Later authors used one or more of these characters but failed to add better discriminating features. For instance Stitz (1939) used the shape of the propodeal spiracles, but also the frontal triangle and the relative length of the funicular segments. Bernard (1968) used alitrunk shape and coloration only. Boven (1976) reverted to the definition of the frontal triangle and the ocelli in his couplets. Kutter (1977) used the shape of the propodeum and again the relative length of the funicular segments, the definition of the frontal triangle and the ocelli. Only coloration, shine and pubescence were used by Collingwood (1978). The latest published keys reverted to the form and position of the propodeal spiracles as the best character (Bolton & Collingwood, 1975; Collingwood, 1979) and additionally the definition of the ocelli (Agosti & Collingwood, 1987).

All this inconsistency in use of the older key characters indicates that they were either not entirely trustworthy, or were indistinct or difficult to discern, rendering discrimination of the two genera difficult.

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During recent studies we have established that the form and position of the propodeal spiracles and the shape of the frontal carinae are good enough to separate both genera unequivocally, but the characters are difficult to describe or perceive. During the survey several new characters were discovered, which allow us to distinguish between *Formica* and *Lasius* easily and definitely. These characters include the construction of the first gastral segment, the articulation of the petiole with the alitrunk and the distribution of setae on the hind tibiae.

These new features are offshoots from a project to discover strong new characters with which to redefine the genera and species-groups within the Formicinae.

Descriptions

The analysis is mainly based on material available at the British Museum (Natural History), London, and includes representatives of all the genera (and most of their included species-groups) of the subfamily Formicinae.

To observe the new characters, the ants must be mounted at the tip of a card-triangle, so that only the pro- and mesocoxae are glued down, leaving the petiole and gaster freely projecting and not at all obscured. It is also best to have the hind coxae directed forward or at least sideways, so that the petiole and gastral base are fully exposed.

First gastral segment (Figs 1, 2). The first gastral segment (= the third true abdominal segment) consists of a smaller sternite and a larger tergite. The tergite overlaps the sternite and also overlaps the base of the second tergite posteriorly. They are linked by interscleritic membranes which allow the expansion of the entire gaster for storage and transport of liquid nutrition. Anteriorly the first tergite is downcurved and narrowed, terminating in a reduced pretergite (= helcium (Figs 1, 2)), which is inserted in the posterior foramen of the petiole. The helcium, the gastral part of the joint, is dorsally collar-shaped in front view, forming a threequarter arc arising from the lowermost anterior part of the tergite. The ventral sclerite of the helcium is an insignificant looking, small plate. In its general state this is a part of the sternite, and has one or two groups of proprioceptor sensillae (for definition and discussion see Bolton (1990)). Apart from the presternite the main part of the sternite is a simple plate, slightly bent dorsalward.

The spiracles of this segment are set towards the anterior ventral

edge of the tergite.

The structure of the first gastral segment of *Formica* and *Lasius* is very distinct. In both the helcium is set low down on the anterior face of the gaster, but this is achieved in a different way in either genus.

In ventral view of *Formica* species the whole anterior face of the first tergite is evenly expanded ventrally, and extends onto the ventral surface. The median section, bearing the helcium, does not project further ventrally than do the portions on each side. The tergite and sternite meet ventrally in a distinct transverse fissure or suture which runs across the width *behind* the sternal plate of the helcium (Fig. 1). This fissure separates the helcium from the sternite proper and the tergosternal junction runs more or less transversely behind the helcium before curving posteriorly to run the length of the segment; the tergosternal junction does not intercept the helcium.

In ventral view of *Lasius*, on the other hand, the median portion of the anterior face of the first tergite, which bears the helcium, projects further ventrally than do the portions on each side (Fig. 2). In consequence the tergosternal junction on each side runs forward from the helcium, then passes through a narrow arc or sharp curve before running back down the length of the segment. Centrally the tergosternal junction intercepts the sides of the helcium and there is no transverse fissure separating the helcium from the sternite proper (Fig. 2).

This is a very distinctive character which shows hardly any variation within the genera; it also functions at genus-group level. The significance of these modifications is discussed below in the section dealing with the petiolar syndrome.

Petiolar syndrome/Gastral reflexing system (Figs 3–8). The petiolar syndrome is a complex of three congruent characters, involved in the articulation of the petiole with the alitrunk. These are: relative depth of the articulatory excavation of the petiole (Figs 3, 4), relative position of the hind coxae (Figs 5, 7), and cross section of the ventral part of the petiole (Figs 6, 8).

The articulatory excavation of the petiole. This is situated posteroventrally on the fused mesometathoracic sternite, between the hind coxal cavities. In *Formica*, the excavation does not reach a line spanning the anteriormost points of the metacoxal cavities (Fig. 3). In *Lasius* the excavation extends anteriorly far in front of this line (Fig. 4).

The relative position of the hind coxae. Seen in ventral view, the mesocoxae form a right angle to the midline and the hind coxae are oriented in a 135° angle. In both genera the mesocoxae are set close together. In Formica the hind coxae are also closely set, forming a V-shaped surface posteriorly (Fig. 5); in Lasius they are separated as wide apart as a petiole width and together with the mesocoxae they form a U-shaped cavity (Fig. 7). In consequence, the cross-section of the petiole in Formica is keeled (Fig. 6) whereas in Lasius it is rounded (Fig. 8), to accommodate the petiole against the metacoxae when the gaster is reflexed.

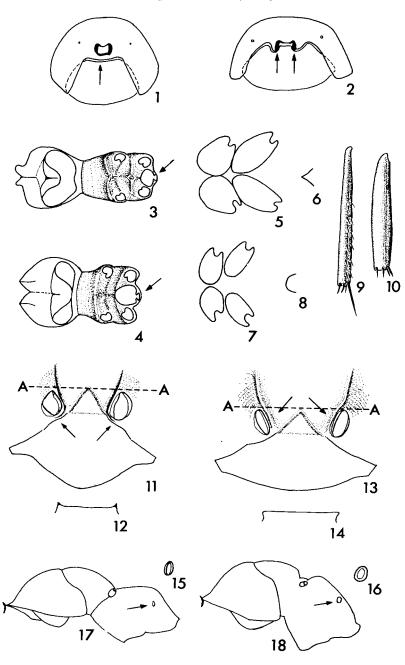
The petiolar syndrome is consistent within *Formica* and *Lasius*. It also seems to be a character of use in defining genus-groups or

tribes within the Formicinae (Agosti, in prep.).

From a functional point of view, the petiolar syndrome can be understood, together with the form of the first gastral segment, as a part of the gastral reflexing system. Fixation of the petiole is needed to keep the gaster in an exactly defined position when preparing either to spray (Formicinae, Dolichoderinae) or to sting (Ponerinae, Myrmicinae), and this can be done in several different ways (Bolton, research in progress). Formica and Lasius represent just two systems out of many. In both these genera it is characteristic that the helcium is situated ventrally on the anterior face of gastral segment one. The fixation of the gastral position is achieved by the ventral shape of the petiole which fits exactly into its counterpart, either the posterior surface of the two closely set hind coxae in Formica (Figs 5, 6), or the U-shaped cavity due to the widely separated hind coxae and closely set mesocoxae, as in Lasius (Figs 7, 8). In each case these interlocking parts serve to hold the gaster in a fixed position when reflexed.

Bristles of the hind tibiae (Figs 9, 10). The hind tibiae of most of the Formicinae have two to several apical bristles. This is the condition seen in *Lasius* (Fig. 10), where it is often also accompa-

Figs 1-18, 1. Ventral view of a gaster of the Formicaconfiguration; arrow indicating the fissure between the anterior and posterior portions of the sternite. 2. Ventral view of the gaster of the Lasius-configuration; arrow indicating fusion of tergite and sternite. 3. Ventral view of the meso- and metathorax of Formica spp.; arrow indicating articulatory excavation of the petiole. 4. Ventral view of the meso- and metathorax of Lasius spp.; arrow indicating articulatory excavation of the petiole. 5. Meso- and metacoxae of Formica spp. 6. Cross-section of the ventral part of the petiole of Formica spp. 7. Meso- and metacoxae of Lasius spp. 8. Cross-section of the ventral part of the petiole of Lasius spp. 9. Hind tibia of Formica sp. 10. Hind tibia of Lasius sp. 11. Frontal part of the head of a Formica sp.; arrow indicates beginning of the frontal carinae; A----A showing the plane of the section of Fig. 12. 12. Section of the frons, showing the angular and prominent frontal carinae in Formica sp. 13. Frontal part of the head of a Lasius sp.; arrow indicating beginning of the frontal carinae; A-----A showing the plane of the section of Fig. 14. 14. Section of the frons, showing the rounded and inconspicuous frontal carinae in Lasius sp. 15. Propodeal spiracle of Formica sp.; note the slitshaped lumen. 16. Propodeal spiracle of Lasius sp.; note the parallel-sided sclerite. 17. Alitrunk of Formica sp.; arrow indicating the propodeal spiracle. 18. Alitrunk of Lasius sp.; arrow indicating the propodeal spiracle.



nied by a thick appressed pubescence. In contrast, *Formica* has an additional double row of bristles on the sides of the ventral surface of the hind tibiae (Fig. 9).

The bristles are distinctly separated and thicker than the underlying pubescence and often of the same shape and colour as the terminal bristles. Sometimes their number is reduced, but in such cases the loss is from basal to apical. An entire loss of the bristles is only recognized in some species of the *F. exsecta*-group, but in such cases there is no thick decumbent or appressed pubescence developed.

This character is very reliable. Except for the above mentioned species of the *F. exsecta*-group there are no other exceptions known.

The systematic use of this character also applies above genuslevel. Within the Formicinae, this particular *Formica*-like arrangement of bristles is only found in some *Melophorus* spp., many *Camponotus* spp., few *Myrmecocystus* spp. and in most of the Formicini.

Frontal carinae (Figs 11–14). The frontal carinae form the lateral limits of the frons. In Formica they begin at the level of the anterior portions of the toruli, run backwards past the toruli and frontal triangle, and end near the level of the anterior margin of the eye. They are either parallel or slightly divergent posteriorly (Fig. 11), and sometimes somewhat curved. They always form distinct, sharp crests which are angular and prominent in section (Fig. 12). In contrast, the frontal carinae in Lasius are bluntly rounded in section (Fig. 14). In Lasius they emerge medially to the toruli where the two toruli are closest set (Fig. 13). They are hardly ever longer than $3\times$ torulus diameter and form only a smooth ridge, without a distinct crest (Fig. 14).

This character is possibly variable at genus-group level. Within *Formica* and *Lasius* there is slight variation present. Nevertheless, within *Formica* there is always a crest on each frontal carina present, whereas this never occurs in *Lasius*.

Propodeal spiracles (Figs 15–18). The shape and the position of the propodeal spiracles differ in both genera. The general form of the spiracle in Formica shows an oval to somewhat slit-shaped outline, and the inner margin of the annular sclerite is never parallel to the outer (Fig. 15). The spiracles in Lasius are round, the inner and outer margins of the annular sclerite always being parallel (Fig. 16). Sometimes spiracles in Formica approach a round form, and spiracles in Lasius may be slightly oval, but even in these cases they are separable by the configuration of the annular sclerite.

The spiracles are set close to the anterior margin of the propodeum in *Formica* (Fig. 17). In *Lasius* the spiracle almost touches the declivitous face of the propodeum (Fig. 18).

Again, both characters seem to be variable at genus-group level, and possibly even at higher taxonomic levels within the Formicinae. They seem to be congruent with certain alitrunk configurations (the *Lasius* configuration with a short metanotum-propodeum and the propodeum often truncated; the *Formica* configuration with an elongate metanotum-propodeum and a domed propodeum). Within the Formicinae round spiracles are the predominant form. Slit-shaped spiracles are restricted to some *Melophorus*, *Camponotus*, all Formicini and some others. However, at genus level and for the purposes of this paper, they separate both *Formica* and *Lasius* quite reliably.

Conclusion

The characters described above not only clearly separate ants of the genera *Formica* and *Lasius* (see newly proposed couplet below) but also have some phylogenetic implications. The gastral reflexion system, the bristles on the hind tibiae, and the construction of the frontal carinae, are all characters at genus-group level. Their use in separating these two genera thus indicates that both genera must belong to two different genus-groups or tribes. Even recently some authors (e.g. Wheeler & Wheeler, 1985) listed *Formica* and *Lasius* within the single tribe Formicini. This seems incorrect and due to reliance on overall habitus similarity, which does not indicate real relationships. A phylogenetic analysis of the Formicini and a discussion of its possible sister-group (Lasiini) is not the aim of this study, but will be presented in a later publication (Agosti, in prep).

New couplet for workers

- First gastral segment of Formica configuration (Fig. 1). Propodeal spiracles slit-shaped to oval, if the latter then the inner margin of the annular sclerite not parallel to the outer (Fig. 15); spiracle located far in front of the posterior propodeal margin (Fig. 17). Hind tibiae with a double row of distinct bristles (Fig. 9), never thickly pubescent. Ventral surface of petiole keeled (Fig. 6). Frontal carinae beginning at the front of the torulus, close to the posterior margin of the clypeus (Fig. 11); each forming a distinct sharp ridge in section (Fig. 12). In ventral view the hind coxae meeting medially (Fig. 5). Cavity of the petiolar insertion in the metasternum at most reaching the midlength of the metacoxal cavities, never projecting forward beyond the level of the metacoxal cavities (Fig. 3).
- First gastral segment of Lasius configuration (Fig. 2). Propodeal spiracles round (Fig. 16) to weakly ovate, if the latter then the inner and outer margins of the annular sclerite parallel; spiracle located close to the posterior propodeal margin (Fig. 18). Hind tibiae without a double row of bristles

(Fig. 10), often thickly pubescent. Ventral surface of petiole rounded (Fig. 8). Frontal carinae arising between the toruli and not longer than two torulus diameters (Fig. 13); frontal carinae rounded in section (Fig. 14). In ventral view, the hind coxae widely separated, forming with the two middle coxae a U-shaped opening (Fig. 7). The cavity of the petiolar insertion in the metasternum reaching at least to a line drawn between the anteriormost points of the metacoxal cavities (Fig. 4).

Lasius

References

Agosti, D. (in prep.). The phylogeny of the ant tribe Formicini with a redescription of the constituting genera, including a new genus.

Agosti, D. & Collingwood, C. A. 1987. A provisional list of the Balkan ants (Hym. Formicidae) with a key to the worker caste. II. Key to the worker caste, including the European species without the Iberian. *Mitt. schweiz. ent. Ges.* **60**: 261–293.

Bernard, F. 1968. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale et septentrionale. Faune de l'Europe et du bassin Méditerranéen 3: 411 pp.

Bolton, B. 1990. Abdominal characters and status of the cerapachyine ants. *J. nat. Hist.* 24: 53–68.

Bolton, B. & Collingwood, C. A. 1975. Hymenoptera, Formicidae. *Handbk Ident. Br. Insects* **6**(3c): 34 pp.

Boven, J. K. A. van 1976. De Mierenfauna van Belgie (Hymenoptera: Formicidae). *Acta zool. path. antverp.* **67**: 1–191.

Collingwood, C. A. 1964. The identification and distribution of British ants. 1. A revised key to the species found in Britain. *Trans. Soc. Br. Ent.* 16(3): 93–114.

Emery, C. 1925. Hymenoptera. Fam. Formicidae, Subfam. Formicinae. *In* Wytsman, P., *Genera Insect.* 183: 302 pp., 4 pls.

Forel, A. 1874. Les fourmis de la Suisse. Neue Denkschr. Allg. schweiz. Ges. ges. Naturw. 452 pp., v + 2 pls.

Kutter, H. 1977. Hymenoptera, Formicidae. *Insecta helv.* 6: 298 pp.

Mayr, G. L. 1861. Die Europäischen Formiciden. Nach der analytischen Methode bearbeitet. 80 pp., 1 pl. Wien.

Stitz, H. 1939. Hautflügler oder Hymenoptera. 1: Ameisen oder Formicidae. *Tierwelt Dtl.* 37: 428 pp.

Wheeler, G. & Wheeler, J. 1985. A simplified conspectus of the Formicidae. Trans. Am. ent. Soc. 3: 255–264.